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THE ORIGIN OF VARIATIONS

SYMPOSIUM AT THE THIRTY-NINTH ANNUAL MEETING OF THE AMERICAN SOCIETY OF NATURALISTS, TORONTO, DECEMBER 29, 1921

VARIATION IN UNIPARENTAL REPRODUCTION

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DARWINISM left the origin of variations the unsolved problem. Give us inherited variations, it said, and we can explain adaptation, by natural selection. But this was the omission of 99 per cent., if not 100 per cent., of the problem of evolution. Are we in better case to-day? Has the experimental study of genetics given us some solid knowledge of the origin, the causes, of variation? Have we learned that the obvious differences observable everywhere among individuals are the foundations of evolution? Or that they are not? Are slight quantitative fluctuations the material out of which evolution is made? Have we discovered that extensive saltations are the steps in evolution? Or that less extensive mutations, qualitative or chemical changes, that may be minute or large, are that by which evolution is constituted? Do we know the origin of such saltations, mutations? Have we found that the present constitution of the organism predetermines in some way the course of further change; or that an *élan vital* is driving the organism to unfold in a definite way, like a flower; that evolution is orthogenesis? Do we comprehend the nature and causes of such a push to unfold, and of the direction in which it tends? Have we found perhaps, as at least one investigator maintains, that it is mixing of stocks, hybridization, that is the origin of organic diversity? Or do we know that the physical and chemical conditions of the environment produce changes that are inherited and give us evolution? Or finally, do several or all of these methods of action concur?

Such are the questions, I take it, on which we hope for light in the discussion this afternoon, and in the discussion of orthogenesis before the American Society of Zoologists, and of the species concept before the Botanical Section of the American Association.

The lines of attack on the problem of variation are as manifold as are the questions to be answered. The basic idea in that attack whose results I shall try to summarize is this: In the reproduction from two parents familiar to us in higher animals and plants, there is a mixing of different stocks, a formation of great numbers of diverse groups of the hereditary materials, with consequent production of a great variety of diverse offspring from a given pair of parents. This is the chief cause of the differences everywhere observable among individuals: differences formerly classed as variations and considered the material of evolutionary change. But such kaleidoscopic regrouping of materials, the units of which are not changing, has no obvious relation with evolutionary variation; in the next generation a new grouping of the same material occurs, and so on indefinitely. If there likewise occur progressive evolutionary changes, these are so lost, so hidden, in the multitude of kaleidoscopic recombinations that they can not be distinguished; the literature of evolution is filled with confusion due to this difficulty.

Therefore the idea suggests itself: Why not avoid at once all this, by studying evolutionary changes in those organisms where no mixing of stocks is occurring; where there is no kaleidoscopic regrouping of the hereditary materials? There are organisms that reproduce from a single parent, with no shifting or recombination of the germ plasm; in these, actual changes that persist from generation to generation, such as evolution requires, should lie open before us, unconfused. We should see evolution occurring, as we see water flowing.

This plain, simple and optimistic maxim has, I fear, like many another such, not proved so illuminating as its promise. But led by it, investigators set themselves at the study of the passage of generations, with selection and propagation of individuals showing diversities, in these creatures where seemingly all lasting change from parent to offspring must be evolutionary. Their hope was to see evolution occurring. And what did they see? I need not review the details; Johannsen, Barber, Hanel, the present writer, Lashley, Agar, and others, followed for long periods the passage of generations in many different organisms during uniparental reproduction.

Their report, after years of work, was astonishingly simple and clear. As to the origin of hereditary variations, it resembled the famous chapter on the Snakes of Ireland. It summed itself, in effect, in the succinct, sufficient, exhaustive proposition that there is no inherited variation; hence no origin of such variation. There is nothing to find out about it, for it doesn't occur. The individuals produced in uniparental reproduction may indeed differ, but these diversities are transitory effects of environmental differences; they are not inherited. All the descendants of a single individual are genetically and hereditarily alike; they form in effect a set of identical twins. And from this it could be concluded that in biparental reproduction *all* the observed diversities are due to the kaleidoscopic regrouping of hereditary materials; nothing to evolutionary change.

Outcries—objurgations and acclamations—greeted these propositions. Some reviled them for their manifest absurdity, others acclaimed them for their obvious truth and the clarification they wrought. Opponents tried to disprove them by investigating the matter themselves; their evidence strengthened the propositions they had thought to overthrow; who came to scoff remained to mourn.

Such was, in the gross, the upshot of the first phase of the study of uniparental inheritance; of perhaps the first ten years. But the matter could not rest here. This work cleared the ground. It showed that 99 per cent. or more of what had been called variation had nothing to do with evolutionary change—a conclusion which Mendelian study was reaching independently. Now it remained to accept that fact, to take a new hold, to grapple with the more difficult question: Is there yet an infinitesimal residuum of evolutionary change? If we select the most favorable organisms, and study them in most minute detail for sufficiently long series of generations, shall we indeed find that there are no persistent variations whatever? Such is the work that has in this field occupied, with redoubled intensity, the last ten years. What are the results of this second phase of the work?

Some of the workers devoted themselves to observational breeding work on the passage of many generations, accompanied by selection; others attempted to modify the inherited characters by physical and chemical agents. In the observational search for persisting alterations, with the attempt to accumulate their results by selection, we find, first, that many of the organisms studied have as yet defied all attempts to find any inherited variations. Such is the report of Ewing on his extended work with aphids; such is the case with the fungi studied by Brierly (1920). Such is the case with most of the strains of the infusorian *Paramecium,* studied in detail for long periods by many different observers. Only in certain deformed strains, and possibly in one or two other instances, has the occurrence of persisting variation been observed in animals living under the usual conditions. Such is the case with the great majority of the strains of the Cladocera studied with such extraordinary thoroughness for long periods by Banta (1921); out of 16 strains to which selection was applied for many generations, all but one gave on the whole negative results; they did not change. Some of the investigators still insist that this is indeed the outcome of all this work; that all cases seeming to give other results are for one reason or another deceptive; that no hereditary variations occur; that evolutionary change has not been observed in this sort of reproduction—and presumably therefore in no other sort. Thus, for example, argue Brierly (1919), and, in effect, Victor Jollos (1921).

On the other hand, in some of the organisms studied, visible changes persisting from generation to generation of uniparental reproduction have been observed. Even in the first period of this sort of work, extremely rare "mutations" were reported by Barber in his work on bacteria, an apparent single one by Lashley in *Hydra;* a "bud variation" or two by Johannsen; and other isolated cases occurred. In the second period of the work, as a matter of observational fact, whatever the interpretation, it is certain that in the lowest Rhizopoda: in *Difflugia,* in *Centropyxis,* in *Arcella;* in the infusorian *Stylonychia,* and in certain abnormal strains of *Paramecium,* as studied in our laboratory at the Johns Hopkins University, there arise in uniparental reproduction, changes affecting both physiological and structural characters; changes that may be very slight, or of great extent; that are passed on to later generations in uniparental reproduction. By selection and breeding of the changed individuals, stocks are isolated which differ persistently from the stock with which the work of breeding began. In this way might well arise the diverse biotypes found in nature to occur within a species, in these organisms. Something similar was found by Stout in the propagation of certain plants by cuttings.

Again, among the 16 strains of Cladocera, subjected by Banta to selection for a physiological characteristic, one, and only one, showed persisting alterations, accumulated by the selective process, so that from the single strain, two continuously diverse strains were produced. Jollos too has observed a few cases in which strains of *Paramecium* became differentiated in ways that could hardly be considered the result of environmental action. Doubtless some other cases might be collected. Here then we seem to have what we were searching for; here at last is something solid; here by our presuppositions we have evolution evolving; we have *seen* it! But as with so many of the seeming solid things of science—so these became sicklied o'er with a pale cast of thought, of doubt, of speculation. What, it is asked, is the cause, the fundamental nature, of these persistent changes? And are they indeed of a sort to be considered steps in evolution?

And when we look closely, the observational and selectional work has given us little information on these points. In *Arcella* Hegner found that certain of the inherited structural changes are mere results of increase or decrease in number of nuclei, brought about in a simple manner. But most of the changes in the lower organisms studied can not be accounted for in this way. The work of Erdmann (1920) indicates that certain persistent changes occur in *Paramecium* as a result of the periodic nuclear reorganization called endomixis. These would perhaps have only a significance similar to that of the recombinations occurring in biparental inheritance. It is a favorite speculative idea with opposing speculators that most or all of the persisting changes we have mentioned arise through irregularities in nuclear division, and hence are of little evolutionary significance, but this is thus far a mere possibility, without solid base; as the Germans say, it floats in the air. Another speculative notion is that the changes lack permanence; that if followed for a sufficiently great number of generations there would be reversion to the original condition. Whether this doubt can ever be resolved by observation can not be predicted; it depends perhaps on the number of generations demanded by the doubters.

In the attempts to modify inherited characters by physical and chemical agents, more positive evidence as to the cause of variation has perhaps resulted. Can we not, it is asked, by subjecting the hereditary material to chemicals, to physical agents, alter it, as we can alter practically everything else in nature? Of course we can; it is easy. But when we alter it we usually kill it, or prevent it from developing; our task is like that consummation devoutly to be wished, of killing the pathogenic bacteria in a man—which is easy—but it also kills the man! Have we succeeded in so altering the germ plasm, without killing it, that it now develops differently, and transmits the diversity to its progeny?

It is easy by altering the chemical and physical conditions to change tremendously the development and characteristics of these creatures, and that without stopping life and reproduction. But in the infinitely greater proportion of cases such changes have no inherited effect; so soon as these particular conditions are removed, the progeny go back at once to the usual constitution. Such has been the result of extensive experiments of my own in modifying *Paramecium* with chemicals; and of Noyes in modifying Rotifera. Startling transformations of form, structure and function are readily produced and kept up for generations, but disappear when the offspring are reared under normal conditions. Once in our work the task seemed accomplished. After many generations of treatment with alcohol, *Paramecium* yielded monstrosities and deformities, analogous to those Stockard obtained by the same method in guinea pigs, and these deformities were transmitted after removal from alcohol, for generation after generation. This was stirring; all the energy of the laboratory was devoted to following the monstrous stock through long periods, leaving the formulation of pedigrees till time permitted. But when this could be done it appeared that all these abnormal individuals came from one single ancestor, out of the hundreds with which the experiment began; the rest had all returned at once to normal. We know that such hereditarily abnormal stocks occur at times in *Paramecium*, produced in some frequency by an agency which takes the matter at once out of the field with which I am dealing —by the recombinations occurring at conjugation, at biparental reproduction. Our monstrous stock may have come from such an individual, included by accident in the experiment. Our spirit-stirring results faded into nothingness—a type of what has so often happened in promising work in the inheritance of environmental effects, of what will probably often happen again.

Other workers have been more successful. In the bacteria, if we can accept the accounts given by many investigators, and well summarized, for example, in Adami's "Medical Contributions to the Theory of Evolution," environmental conditions frequently alter, in an adaptive way, the persisting characteristics of the stocks, differentiating a single race into several. The difficulties of certainly working with unmixed strains is very great in these minute creatures, a fact which leads many students of experimental evolution to reject generalizations based on these organisms. Further, the extraordinary work of Löhnis (1921), recently published by the National Academy, tends, if substantiated, to so completely upset all supposed knowledge of life history in the bacteria that it will be best to omit these from consideration until the air is cleared. For similar reasons, and from considerations of space, I will not speak of the work on pathogenic Protozoa.

Turning then to those larger organisms that are isolated with as much ease as are guinea pigs, Middleton has found that differences of vigor and of rate of reproduction are produced by subjection of infusoria for long periods to diverse temperatures, and are perpetuated, after equalizing the temperatures, from generation to generation for long periods, and through the process of conjugation. At this meeting he has reported similar results produced by subjection to diverse chemicals. How far this is comparable to change of other characteristics than reproductive vigor we do not know.

Victor Jollos (1921) has just published in this field work which must make a deep impression on the study of experimental evolution, work which gives us more positive results than have before been achieved. By experimentation extending over years he has, by subjection for long periods of time, altered the resistance of the infusorian *Paramecium* to certain chemicals, and to heat. After removal of the causative agent these physiological changes are passed on from generation to generation of uniparental reproduction, for longer or shorter periods. Of extreme interest is the fact that longer subjection to the altering agent causes longer persistence after the agent is removed. The induced changes lasted in some cases for hundreds of generations, not yielding at the periodic nuclear reorganizations known as endomixis. But the acquired resistance in practically all cases finally disappeared if the organisms were continued sufficiently long in the normal conditions. Subjection to frequently varied environment hastened the disappearance of the persisting effect; and it usually disappeared at once when there occurred the profound reorganization accompanying conjugation and biparental reproduction. But in some cases, as in Middleton's results, the acquired resistance lasted through conjugation; even through several cycles of conjugation. But in all cases in which it was clear that he was dealing with resistance acquired through subjection to chemical or physical agents, it finally disappeared, after hundreds of generations, if the organisms were kept sufficiently long in an environment lacking the causative agent. Jollos is from this inclined to draw the conclusion that the changes are not comparable to the (assumedly) permanent differences that separate genotypes or species, and hence that they do not indicate a method by which such permanent differences may arise.

Here emerges an obvious logical difficulty involved in all work on the production of inherited change through environmental action. If we succeed in producing such change, it is clear that the character altered was not a permanent one. And if after long re-subjection to the original environment the induced change disappears, it is equally clear that the new character was no more permanent than the original one. If we now assume that there are other characters that *are* permanent, not alterable by environmental action, of course we can obtain no light on these by changing those characters that can be changed. To me it appears that we have no right to assume, at the present stage in the game, that any such absolutely permanent characters exist. If this be true, then the production of changes persisting through many generations of uniparental, and even of biparental, reproduction, with the further fact that the greater the number of generations the altering agent has acted, the greater the number of generations the change persists, seems of the greatest interest. It perhaps would, if action of the environmental agent continued sufficiently long, lead to production of inherited characteristics that are as permanent as any such characters are. It is certainly, as Jollos agrees, capable of producing such diversity of biotypes as we find within a species; and it might perhaps, if the results of diverse agents are cumulative, produce any of the inherited diversities found in organisms. This is the most promising lead that we have found in the study of uniparental production.[1]

In sum, the study of variation in uniparental reproduction yields the following: The germinal or genotypic constitution in most organisms is extremely stable; in many stocks it changes not at all, so far as observation goes. To alter it by physical or chemical agents is usually to kill it. In some of the lowest organisms—rhizopods, bacteria, some infusoria—it changes with somewhat greater frequency, though still rarely. The nature of the changes, and whether they may be permanent, or must after many generations revert to the original condition, is in some dispute. In these same organisms, environmental agents may produce changes persisting through many generations of uniparental reproduction and even through biparental reproduction, the period of persistence depending partly on the number of generations through which the producing agent acted. This suggests that inherited characters as permanent as any that exist might in time be so produced. In spite of important differences of opinion among investigators, to the reviewer the facts in uniparental reproduction seem to point more toward the production of evolutionary change by the action of the environment on the germ plasm than by any of the other methods. In this respect it takes its place in that modern revival of work on the inheritance of acquired characters, of which we had so striking an example this morning, in the account of the dizzy rats and of the inheritance of their dizziness; though in the study of uniparental reproduction nothing has appeared that indicates a transfer of somatic characters to the germ.

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[1] The important observations and discussions of Jollos relating to changes producible by environmental action at the time of conjugation do not fall within the compass of a discussion of uniparental reproduction.

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